Dependence of the Visual Response Estimated by the Masking Technique on the Stimulus Temporal Luminance Gradient ?. Effects of the Stimulus Spatial Extent and Luminance

著者	TAKIURA Takayuki
journal or publication title	Tohoku psychologica folia
volume	61
page range	29-47
year	2003-07-01
URL	http://hdl.handle.net/10097/54746

Tohoku Psychologica Folia
2002, **61**, 29－47

Dependence of the visual response estimated by the masking technique on the stimulus temporal luminance gradient. I. Effects of the stimulus spatial extent and luminance

TAKIURA TAKAYUKI（滝浦孝之）

(*Japan Society for the Promotion of Science*)[1]

Two experiments were performed to investigate the effects of the rise and decay times, or of the linear temporal luminance gradient of luminance, of the disk stimulus presented at the fovea on the visual responses estimated as the masking curves. With shorter rise or decay times of the mask, the overshoot appeared on the masking curve, whose magnitude and peak position were dependent on the rise or decay time, confirming the results obtained by Matsumura (1976, 1977). With longer rise or decay times, the overshoot disappeared and the whole curve became quite sluggish. These facts suggest that the information on the temporal luminance change at the center of the visual field is transmitted and processed by the magnocellular visual subsystem with shorter rise or decay times of the stimulus and by the parvocellular subsystems with longer ones. The critical luminance transition time advantageous to the magnocellular pathway was assessed at about 250-400 msec, which is independent upon the stimulus luminance. The manner of the change in the shape of the masking curve is essentially independent of the mask luminance and diameter, but is highly dependent on the mask luminance polarity. This fact supports the idea that the luminance increment and decrement are processed by the on- and the off-channels, respectively.

Key words: increment, decrement, masking, rise or decay times.

Introduction

In many vision researches with aperiodic stimuli, measurements have been done using stimuli with rapid rise or decay times, since an abrupt change in luminance is thought to initiate larger responses in the visual system than the slow luminance change. In a different view, however, the temporal waveform of the stimulus, or the temporal rate of the luminance change, can be regarded as an important variable in the research on the temporal response characteristics of vision.

The effects of the temporal stimulus waveform on the visual response have been far less investigated than those of the other stimulus variables. But in the neurophysiological studies, one can find reports on the effects of the temporal stimulus waveform upon the ERG (electroretinogram) of the man and animals (Bartley & Bishop, 1942; Bornschein, 1961, 1962a, 1962b; Bornschein & Gunkel, 1956; Bornschein & Schubert, 1953; Hopp & Penzlin, 1984;

1. Present Affiliation: Department of Human Sciences, Faculty of Humanities and Human Sciences, Hiroshima Shudo University, 1-1-1, Ozuka-higashi, Asaminami-ku, Hiroshima, 731-3195, JAPAN.
[e-mail: takiura@shudo-u.ac.jp]

Ishihara, 1906; Kühne & Steiner, 1880; Penzlin & Hopp, 1985; Ronchi, 1958; Ronchi & di Francia, 1957; Ronchi & Grazi, 1956; Ronchi & Moreland, 1957; Troelstra & Schweitzer, 1963; Wang, 1937), upon the responses of the retinal ganglion cells of the cat (Bornschein, 1962a, Enroth-Cugell, 1961, 1963; Heggelund, Karlsen, Flugsrud & Nordtug, 1989), and upon the human VECP (visual evoked cortical potentials: Clynes, Kohn & Lifshitz, 1964, Sato, 1983). In the psychophysical studies, too, there are some reports on the effects of this stimulus variable upon the temporal summation for the brief pulse of light at threshold (Long, 1951; Rashbass, 1970) and upon the brightness difference threshold for the prolonged stimulus (Drew, 1937; Knau, 2000; Metzger, 1930; Stern, 1894; Takiura, 1996; van der Wildt & Rijsdijk, 1979). In the studies on the spatiotemporal characteristics of the magnocellular and parvocellular pathways, sinusoidal gratings or bars with variable temporal gradient of the contrast have been employed (Bergen & Wilson, 1985; Breitmeyer & Julesz, 1975; Budrikis & Lukas, 1975; Sato, 1984; Stromeyer, Zeevi & Klein, 1979; Tolhurst, 1975; Tulunay-Keesey & Bennis, 1979). But in these psychophysical studies, where detection thresholds or reaction times were measured, only one aspect of the visual response such as the amplitude or the latency may be reflected on these indices. So in the psychophysical studies cited above, contrary to the neurophysiological studies, the change in the whole course of the response with the change of the temporal gradient of the luminance or contrast cannot be explored.

The temporal course of the visual response, especially that at the relatively peripheral stages in the visual system, is believed to be able to recorded psychophysically as the masking curve (Boynton, 1972; Boynton & Siegfried, 1962; Hood, 1998) measured by the technique of the masking of light by light (Breitmeyer, 1984). In the experiment of the masking of light by light, the detection thresholds for the brief probe pulse are measured at variable delays relative to the moment of the luminance change introduced by the stimulus called mask or masking stimulus presented on the adapting background. The probe and the mask are usually spatially uniform circular disks and are spatially concentrically presented. The obtained thresholds are plotted in logarithmic form as a function of the temporal delay, which is referred to as the masking curve. The probe threshold begins to rise about 100 msec before the presentation of the mask, and reaches its peak at and near the time of the luminance change caused by the presentation of the mask (the increment or the decrement in luminance) to form the transient overshoot. After the moment of the luminance change, the threshold falls rapidly at first and then gradually to reach an asymptotic level. When the mask is as brief as 50 msec or less, the threshold overshoot is observed only at and near the preceding edge of the luminance change. The masking curve is to evaluate sensitivity changes in the visual system introduced by the stimulus presented on the adapting background, and can be thought to be the trace of the response of the earlier stages of the light or dark adaptation mechanism to the change in the ambient illumination level or to be the indirect record of the response waveform of the on- or the off-channels.

Using the technique of the masking of light by light, Matsumura (1976) investigated the effects of the rise or decay time of the prolonged mask upon the time course of the visual response. For the test of the effects of the rise time, the incremental mask of 2516 td in illuminance and with linear rise time of 0, 50, 100, or 200 msec was presented on the adapting background of 624 td.

To test the effects of the decay time, the decremental mask of the illuminance of -2516 td with linear decay time of 0, 50, 100, or 200 msec was presented on the adapting background of 3140 td. The adapting background and the mask were both 6.73 deg in diameter, and the probe was 1.72 deg in diameter and 2 msec in duration. As the rise time of the mask was increased, the threshold overshoot at the time of the mask presentation was decreased in magnitude, and it also tended to be delayed accordingly. The delay of the peak of the overshoot was 5-10 msec at the instantaneous luminance transition, and was 30-40, 40-50, and 50-60 msec with the rise time of 50, 100, and 200 msec, respectively. The shape of the threshold overshoot varied with the rise time of the mask. The longer the rise time was, the less sharp the overshoot was. The sub-peaks appeared with the longer rise times as 100 and 200 msec. They seem to appear at about 100 msec of the delay with the rise time of 100 msec, and at about 150 msec and maybe also at 250 msec with 200 msec rise time, though Matsumura (1976) made no suggestion of their positions. With variations in decay time, only slight changes in the magnitude of the overshoot at and near the moment of the luminance change were noticed in contrast to the case of the rise time. The temporal position of the overshoot was delayed according as the increase of the decay time. The delays of the occurrence of the overshoots were, however, smaller than those with variations of the rise time, and were 30 msec at the most with the longest decay time. The more the decay time was, the more slowly the overshoot decayed. Similar results were also obtained from the experiment with more limited luminance and temporal conditions, except the gradual temporal lag of the occurrence of the overshoots and, for the magnitude of the overshoots, the relative independence of the decay time of the decremental mask (Matsumura, 1977).

Based on these findings, one might be able to partly explain the results of Cogan (1992), who measured the duration of just detectable break in the luminance ramps. Cogan used luminance incremental and decremental ramp presented upon a uniform adapting background with 7.5 deg in diameter and 2000 td in retinal illuminance as stimuli and measured the duration of just detectable break presentd at a half-height of the total illuminance change (495 td). The duration of just detectable break was decreased with the increase of the rise or decay time, reaching its minimum of about 30-60 msec, which does not include the break time, at about 100 msec and increased with the longer rise or decay time.

If such break threshold is determined by the occurrence of the response to the luminance ramp after the break, Cogan (1992)'s results with the luminance incremental ramp might be explained in the following way. With the rise time of about 100 msec, the duration of the first ramp is about 50 msec and the peak of the response evoked might be located at the delay of about 30-40 msec, based upon the results reported by Matsumura (1976). This response decays relatively rapidly, so the retinal sensitivity recovers significantly before the presentation of the second ramp. With the shorter rise time than 100 msec, the response peak for the first ramp will be located at the temporal point after the first ramp and this response masks the response to the second ramp, causing the increase of the break threshold. With the longer rise time than 100 msec, the response to the first ramp will be evoked during the first ramp, but its amplitude decreases and its temporal course slows down, which makes the separation of the response to the second ramp and that to the first ramp difficult. So the break threshold increases. The results of

Cogan (1992) with the decremental mask might be explained in a similar way on the basis of Matsumura (1976)'s data.

The generality of the results of the Matsumura (1976, 1977)'s experiments, however, is unclear. Matsumura carried out his experiments with considerably high luminance of the mask and the adapting background, and with larger size of the probe than those usually employed in the masking experiments (e.g. Boynton, Bush & Enoch, 1954; Kitterle & Leguire, 1980; Poot, Snippe & van Hateren, 1997). In addition, the data from one of Matsumura (1976)'s observer (HI) showed no tendency of the delay of the threshold overshoot with the increase in the rise time of the incremental mask.

In order for our knowledge on the effects of the rate of the stimulus luminance change on the visual responses psychophysically-estimated as the masking curve to be more firm, we conducted the experiments designed to replicate Matsumura (1976, 1977)'s measurements, changing the spatial extent of the mask, the mask luminance, and the luminance level of the adapting background. We also performed an experiment comparing the effects of the change of the temporal luminance gradient with those of the change of the luminance to investigate whether these two stimulus variables affect the same mechanism of temporal vision.

In the present paper, we report the experiments on the effects of the mask diameter and luminance. The ramp duration was ranged between 0 and 400 msec, which included the rise or decay times longer than those employed by Matsumura. The report of the experiments on the effects of the adapting background luminance and on the difference in the effect between the change of the temporal luminance gradient and the change of the luminance will appear in the next volume of this journal.

EXPERIMENT 1: Effects of the stimulus diameter

Matsumura (1976, 1977) obtained the masking curves using the mask and the probe of 6.73 deg and 1.72 deg in diameter, respectively. The form of the masking curve might be affected by these relatively large dimensions of the stimuli in such a manner as the speed-up of the responses to the incremental mask by the spatial summation of the luminous energy (Wilson, 1997). In the present experiment, the threshold was determined for the circular probe of 0.43 deg in diameter, the size of which is common to the usual masking experiments, presented at various times with respect to the moment of the presentation of the mask whose diameters were in the range from 0.86 to 10 deg.

Methods

Observers

Three undergraduate students, HA, SH, and TT, whose ages were ranged between 22 to 25 years, from Tohoku University served as observers. All of them had normal or corrected-to-normal visual acuity.

Apparatus and stimuli

Two channels of the four-channel Maxwellian-view optical system were used for stimulus presentation. The first channel was used for presentation of the adapting background and the mask, and the second one for the probe. The light source of each channel was a glow-modulator tube (Sylvania, R1131C), which was constantly operated at 25 mA and was always provided with the quiescent current of about 10 μA to keep the gas in the tubes ionized and to avoid onset jitter. The outputs of both tubes were constantly monitored by photomultipliers (Hamamatsu Photonics, 931A) and an oscilloscope (Kikusui Electronics, COS5021). Luminance calibration of the optical system was made by the method of Boynton (1966) using the luminance meter (Toshiba, BM-2).

The adapting background consisted of a train of light pulses, each of which was of constant duration of 0.055 msec. The luminance increment or decrement of the adapting background, which is referred to as the mask, was generated by pulse density modulation using the voltage-to-frequency converter (NF Corporation, FG-113) in order to make the color change of the output of the tube as small as possible. The linear ramp-like voltage waveform fed into the input of the voltage-to-frequency converter was generated by the laboratory-made integrating circuit using the op-amp (National Semiconductor, LM301A). The diameter of the adapting background and the mask was 0.86, 1.72, or 10 deg. Since the stimulus was viewed foveally, each of these stimulus dimensions corresponds to the foveal region within the rod-free area, to the retinal area as large as, or slightly larger than, the rod-free area, and to the retinal area containing both rods and cones, respectively (Curcio, Sloan, Kalina & Hendrickson, 1990; Østerberg, 1935). No surround was presented. For the test with the incremental mask, the illuminance of the adapting background was increased linearly over 0, 70, 160, 250, or 400 msec (rise time) to the maximum of 200 td, and 4 sec later it returned to the original level of 100 td. For measurement with the decremental mask, the adapting background of 435 td was decreased in illuminance linearly during the period of 0, 70, 160, 250, or 400 msec (decay time) to the minimum of 335 td, and after keeping this illuminance level for 4 sec, it returned to the initial level. The carrier pulse frequency was 200 Hz for the incremental mask and was 870 Hz for the decremental one. The probe pulse subtending 0.43 deg was presented by directly impressing the glow modulator tube with the rectangular electrical pulse of 2 msec in duration. The probe and the mask were optically superposed concentrically and were presented together at a given delay interval determined according to a randomization schedule. The sequence of the probe-mask was repeated every 8 sec to avoid the carry-over effect of light adaptation. Timing control of the stimulus presentation was made by the electronic stimulator (Nihon Kohden, SEN-6100) with the pulse generator units (Nihon Kohden, EP-601J).

Procedure

Observers were seated in a light-proof, ventilated room and stabilized the position of their heads by a head holder and a chin rest with the biting board arrangement. Before the measurements, they dark-adapted for 15 min first, and then light-adapted to the steady adapting background for 5 min. Observers fixated the stimuli foveally with his dominant eye through the artificial pupil of 2 mm in diameter. The central fixation was secured by employing a fine cross-hair reticle across the adapting background.

In the experimental session, test was done with only one rise or decay time with either of the two luminance polarities of the mask with one diameter. Within a session, the temporal delay of the probe was tested in a randomized order. The session for one stimulus combination was repeated three times on a separate day, though only one session could be run per decay time for HA. Sessions with different temporal gradient were randomly intermixed. After the whole data were gathered with one stimulus diameter, measurements were done with the other diameter for each observer. In each session, two to four thresholds were collected consecutively at each delay interval by the method of adjustment. The observer adjusted the rotation angle of the circular neutral density wedge driven by a stepping motor in order to set the luminance of the probe at threshold. After each threshold determination, the wedge was changed in rotation angle by variable amount by the experimenter to decrease undesirable correlation between consecutive thresholds. Measurements were run over a long period of time, so the observers took rests as they wanted to do so during each session.

Results

The results are presented in Figure 1 with the incremental mask and in Figure 2 with the decremental one. In each figure, the upper and the lower panel includes the results from the different observer, respectively. In these figures, the log threshold illuminance of the probe is plotted as a function of the probe delay in reference to the temporal point at which the mask was presented. Negative values of the delay indicate that the probe was presented before the presence of the mask. The parameter of the graph is the rise time for Figure 1 or the decay time for Figure 2. In these figures, the data for each observer are shifted upwards in arbitrary log units without the case of the smallest mask in order for the family of the graphs with different mask size not to overlap with each other.

As the rise time of the incremental mask is increased, the transient overshoot of the probe threshold is delayed and its magnitude decreases. The magnitude of the overshoot is defined as the difference between the probe threshold at the temporal delay of -100 msec and that at the peak of the curve. The difference in magnitude of the overshoot between the instantaneous luminance change and the second shortest rise time, i.e. 70 msec, however, seems to be relatively small. The temporal position of the peak of the threshold overshoot is 0-5, 20-30, 40-50, and 70-80 msec for the rise time of 0, 70, 160, and 250 msec, respectively. The temporal spread of the overshoot tends to increase with the prolongation of the rise time. With the rise time as long as 250 msec for SH or 400 msec for TT, the threshold overshoot is lost, and the graph is composed of the exponentially rising and the following horizontally lying parts. The transition from the rising part to the flat one does not occur at the end of the luminance change but occurs during the luminance increase except the case for SH for the mask subtending 0.86 deg with the rise time of 250 msec. In this case the probe threshold rises abruptly up to the temporal delay of about 100 msec and then slowly up to 300 msec at which it reaches the asymptotic level. For this observer, the graph for the mask of 1.72 deg with the rise time of 400 msec may also be decomposed into the three components similar to those in this case.

The increase of the mask diameter accompanies no systematic change in the shape of the masking curve. The magnitude of the overshoot is roughly the same for all the mask size including

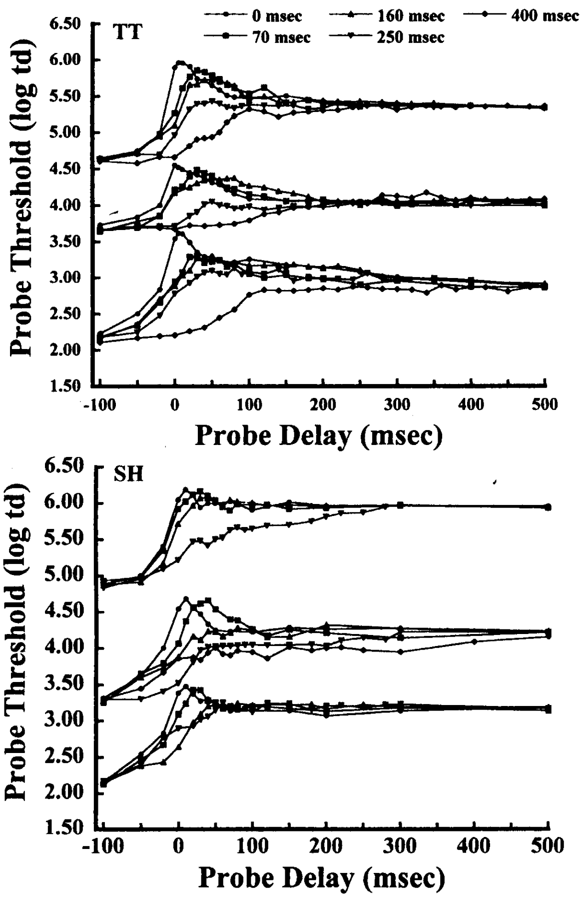

Figure 1. Masking curves for the prolonged incremental mask with variable diameter. The parameter of the curve is the rise time of the mask. Each panel shows results from different observer. The family of the curve with one mask diameter is shifted along the ordinate in arbitrary log units for graphical clarity. In each panel, the top family of the curve shows data with the mask of 10 deg, the middle family with the mask of 1.72 deg, and the bottom family with the mask of 0.86 deg in diameter. The mask was 100 td and the adapting background was 100 td in illuminance.

the one where the rods as well as cones are stimulated but the case with 0.86 and 10 deg masks for TT, where the amount of the threshold change is larger by about 0.4 log units than the case with the 1.72 deg mask for unknown reasons. One possible reason for the higher peaks of the overshoots might be the difference in the time of measurement: for this observer, the measurement with the mask with these sizes was done several months before that with the mask subtending 1.72 deg. The masking curve with the mask diameter of 1.72 deg is roughly the same in shape as those obtained under the same stimulation condition in the following experiments.

The appearance of the sub-peaks in the masking curve pointed out by Matsumura (1976)

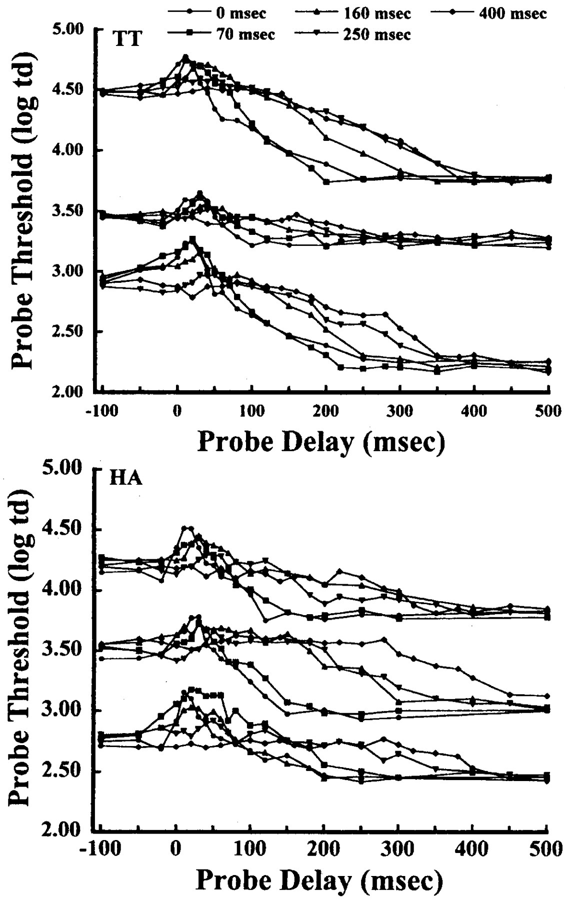

Figure 2. Masking curves for the prolonged decremental mask with variable diameter. The parameter of the curve is the decay time of the mask. The mask was -100 td and the adapting background was 435 td in illuminance. See legend of Figure 1.

with the temporally ramped mask is not systematically in the present data. Only for the curves with 250 msec rise time for TT, the second peak seems to appear over all the mask diameters, which may be comparable with the second peak in the data of Matsumura (1976) with the rise time of 200 msec. Even in this case, however, the third peak, which seems to appear in the result reported by Matsumura, can be hardly noticed.

With the decay time of the decremental mask of 70 or 160 msec, the magnitude of the transient overshoot, which is defined in the same manner as that with the incremental mask, is not so much reduced compared with that with the decay time of 0 msec. It is significantly reduced with the decay time of 250 msec, though the overshoot can be clearly noticed. The peak of the overshoot tends to be located at longer delay as the decay time of the mask increases: it is at about 20-30, 30-40, and about 50 msec for the decay time of 0-70, 160, and 250 msec, respectively. These peak positions are a little delayed in comparison with those in the result of Matsumura

(1976), probably because of the lower luminance of the mask in the present experiment. The extent of the change in the peak position of the threshold overshoot is far smaller for the decremental mask than for the incremental one.

Preceding the overshoot, a small dip is sometimes present in the curves like the backward sensitization reported with the pulsed or step-like incremental mask (Boynton & Miller, 1963; Sperling, 1965), which may be the reflection of the preexcitatory inhibition well established in the retinal neurophysiology.

With the decay time as long as 400 msec, there is little or no rapid transient change in the probe threshold. Only a slow hump of small magnitude is present at the delay of 100-150 msec, if any. The probe threshold keeps being roughly constant up to the delay of about 100-150 msec for TT and up to about 300 msec for HA, beyond which it falls gradually during the period of the ramp, approaching a steady level.

In the data of TT with the mask diameter of 1.72 deg, the magnitude of the overshoot is smaller by about 0.1 log units and the size of the decrease after the peak of the curve is smaller by about 0.4-0.5 log units than those with the other diameters. For HA, the size of the threshold decline following the peak is larger by about 0.2 log units with the mask subtending 10 deg than with other masks. Such dependency of the slope for the family of the curves upon the particular diameter for one observer does not apply to the other's data. This suggests that such dependency is due to some effects of the difference in the time at which the data were obtained among the three diameters for each observer rather than to the genuine effects of the spatial extent of the mask. For TT, the graph with the mask subtending 1.72 deg seems to be roughly the same in shape as those reported in the following experiment under the same stimulation condition. It is desirable to design the experiment so that the data for the critical comparisons are taken in the same session since it seems that the between-sessions variation of the threshold value is larger than the within-session one. Wertheimer (1955) showed that there are reliable shifts in visual absolute thresholds from day to day. In the spatial sensitization task, Buck (1985) reported the result suggesting that the thresholds obtained in the different days differ from each other by as large as 0.2 log units. The results reported by Battersby and Wagman (1959) shows that the masking curves obtained for the brief pulses of light with the same luminous energy but with different durations are different in shape from each other when the measurements were done on separate days. Boynton and Siegfried (1962), however, presented the masking curves of the same shape for two brief stimuli of the same brightness but of the different duration obtained in the same session. In the experiment reported in the present paper, however, the stimulus conditions were so many that all the tests could not be done in the same session.

Discussion

The results obtained in the present experiment show that the prolongation of the rise or decay time of the visual stimulus causes both the decrease in the magnitude of the visual responses and the slowing of the temporal course of the response. This means the decrease in the transient responsibility of the visual system to the gradual temporal luminance change. The role of the mechanisms producing the transient responses at the onset and the offset of the visual stimulus is thought to be the detection of and the emphasis on the temporal luminance change. If so, such mechanisms may respond to the gradual change in luminance in the manner depending upon the rate of the luminance change to encode the temporal structure of the visual stimulus. The decrease in the magnitude of the threshold overshoot with the decrease in the rate of the luminance change is smaller for the decremental mask than for the incremental one. This suggests that the time constants are longer for the mechanism sensitive to the luminance decrement, or for the off-channel, than for the mechanism sensitive to the luminance increment, or for the on-channel, which is consistent with the result of the neurophysiological study on the response of the retinal ganglion cells of the cat (Fischer, Krause & May, 1972).

The effects of the mask diameter on the shape of the masking curve are not systematic at all irrespective of the mask polarity. This fact suggests that the response characteristics of the visual system for the temporal luminance transition are independent of the spatial dimension of the stimulus which is large enough. Battersby and Wagman (1964), Frumkes and Sturr (1968), and Kitterle and Leguire (1975, 1980) showed that the magnitude of the threshold overshoot at the onset or at the offset of the prolonged incremental mask with rectangular waveform is almost independent of the mask size if the distance between contours of the probe and of the mask is large enough to keep the laterally inhibitory interaction between the probe and the mask from occurring. The present experiment confirms these results of the independency of the mask size for the threshold overshoot magnitude with the instantaneous luminance change, and also shows that such independency applies to the case with the gradual luminance transition. For a tiny stimulus of several minutes in diameter, with which the masking curve is difficult to be obtained, visual responses may be different in quality from those evoked by a larger stimulus. Takiura (1996) explored the effects of the rise or decay times of a prolonged stimulus by measuring the brightness difference threshold. The range of the rise or decay time was between 0 and 400 msec. The increase of the rise and decay time led to a rise in the incremental and the decremental threshold, respectively, with stimuli subtending 1.72 deg and larger, but had no effects on the thresholds with stimuli as small as 0.03 deg in diameter. This result can be understood on the basis of the idea of the visual processing by the parvocellular and the magnocellular pathways. Detection of the stimulus may be mediated by the magnocellular pathway with the larger dimensions of the stimulus, and by the parvocellular pathway with the tiny stimulus, since the cells in the magnocellular pathway are more sensitive to higher temporal and lower spatial frequencies than the cells in the parvocellular pathway, which is more sensitive to the higher spatial frequencies in comparison with the cells in the magnocellular pathway (Breitmeyer, 1984; Merigan & Maunsell, 1993). With the mask and the probe of a sinusoidal grating patch, Mitov, Vassilev and Manahilov (1981) reported that the masking curve has sharp transients both at the onset and at the offset of the mask with lower spatial frequency (2 or 6 c/deg), whereas it shows no sign of transients or humps with the higher (18 c/deg) spatial frequency, which is in favor of the idea that the processing mechanisms for the very small stimuli are different from those for the larger ones. This idea is in line with the existence of the parallel visual subsystems of the magnocellular and parvocellular systems. The parvocellular-magnocellular dichotomy may predict the difference in the shape between the masking curve with ramp duration of 250 msec or shorter (for SH, of 160 msec and shorter) and the one with ramp duration of 400 msec (for SH, of 250msec). The shape of the masking curve can be thought to reflect the output waveform of the magnocellular pathway for the rapid change in luminance, or of the parvocellular pathway for the slow luminance change.

Our finding that the decrease of the magnitude and sharpness as well as the increase of the peak delay of the overshoot with the increase of the rise time of the incremental mask is in good agreement with the neurophysiological researches on the photopic ERG of the man or of the ground squirrel (Bornschein, 1961, 1962b), on the on-center Y cells, which are included in the magnocellular pathway, of the cat retina (Bornschein, 1962a; Enroth-Cugell & Jones, 1961, 1963; Heggelund, Karlsen & Nordtug, 1989), and on the human VECP (Clynes, Kohn & Lifshitz, 1964; Mierdel, Zenker & Marre, 1992). The neurophysiological researches on the off-center retinal ganglion cells of the cat, which are probably the Y-cells, showed that the peak firing rate is relatively independent of the increase of the decay time of the luminance decrement (Bornschein, 1962a; Enroth-Cugell & Jones, 1963). This fact is also in agreement with our human psychophysical data.

In the researches cited above, however, the off-center cells give the peak response at the last part of the decremental ramp. Although some cells are found to respond to the exponentially-decaying stimulus with the peak firing at the middle of the decaying part of the stimulus (Enroth-Cugell & Jones, 1963), most cells respond with the maximal response at the end of the decaying part of the stimulus. In the study of the ERG of the rainbow trout for the linearly decaying luminance ramp, it has been reported that the peak of the response is located at the last part or after the ramp (Penzlin & Hopp, 1985). In our psychophysical data, the response evaluated as the masking curve reached its peak in the first part of the luminance decremental ramp. Moreover, with the incremental stimulus the increase of the delay of the occurrence of the threshold overshoot in the present experiment is larger than the increase of the peak latency of the neuronal response of the man, of the cat, or of the ground squirrel (Bornschein, 1961, 1962a, 1962b). So the neurophysiological researches on the retinal responses seem to be in disagreement with our psychophysical finding with respect to the temporal position of the response peak. The relative agreement with the psychophysical data in this point can be found in the human VECP data. Clynes, Kohn and Lifshitz (1964) found that the off-responses of the human VECP are evoked during the period of the 500 msec rapid-on sawtooth. Matsumura (1979) speculated that the information on the rising temporal edge of the luminance increment is conveyed from the peripheral to the central stages by the relatively simple process, while the information on the decremental change in luminance may be transmitted through the more complicated pathways. But we have not encountered the finding supporting this hypothesis at present. This problem is to be solved in the future.

The double-flash illusion (Bowen, Mallow & Harder, 1987) is the visual temporal illusion that a supraliminal single pulse of light appears to be flickering when presented about 70-400 msec after a decremental luminance step. In the present experiment, the optimal delays for the double-flash illusion to be observed are about the same for the decremental step as for the decremental ramp with the decay time of 160 msec. Since this illusion is considered to be caused by the superposition of the two oscillatory responses, that is, the responses evoked by the luminance decrement and by the brief pulse of light (Bowen, 1989), this result is consistent with the finding that the decay time of the stimulus has small effect on the delay of the peak of the threshold overshoot. In the following experiment, observers sometimes reported the occurrence of the double-flash illusion with the decay time as long as 250 msec even when they had no knowledge about this illusion. No report of seeing multiple flashes was obtained with the decay time of 400 msec. These facts suggest that the oscillatory responses are evoked not only by the decremental step but by the decremental ramp with the ramp phase of 250 msec or less in duration.

EXPERIMENT 2: Effects of the mask luminance

In this experiment, the effects of the mask luminance upon the masking effect were investigated. The previous researches employed the masks of 2516 td in absolute illuminance presented on the adapting background of 624 td for the incremental masks, and of 3140 td for the decremental masks (Matsumura, 1976), or the masks of the absolute illuminance of 1256 td on the background of 1884 td (Matsumura, 1977). In the present experiment, the masking curves were obtained with the masks of the lower illuminance to test whether the results reported by Matsumura are specific to the relatively high illuminance of the mask or not.

Methods

Observers

Three undergraduate students, MF, TT, and YN, aged 24 or 25 years, from Tohoku University served as observers. All of them had corrected-to-normal visual acuity.

Apparatus and stimuli

The optical system was the same as that used in Experiment 1. The absolute illuminance of the incremental or decremental mask was 25, 100, or 335 td. The incremental mask was presented on the adapting background whose illuminance was 100 td, and the decremental mask on the background of 435 td in illuminance. The rise or decay times of the mask were the same as those in Experiment 1, that is, 0, 70, 160, 250, and 400 msec. The diameter of the adapting background and of the mask was 1.72 deg.

Procedure

The experimental procedure was the same as that in Experiment 1 except two points: the luminance of the mask was changed instead of its diameter, and the measurement was done with the masks of different luminance randomly intermixed.

Results

The results are presented in Figure 3 and in Figure 4 for the incremental mask and for the decremental one, respectively. The presentation of the data follows the Figures 1 and 2. The data

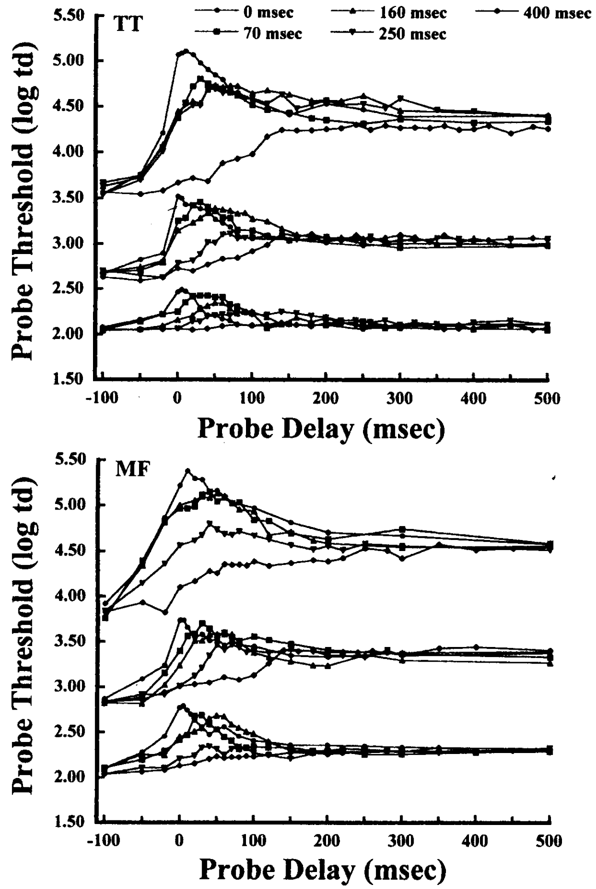

Figure 3. Masking curves for the prolonged incremental mask with variable illuminance. The parameter of the curve is the rise time of the mask. Each panel shows results from different observer. The family of the curve with one mask illuminance is shifted along the ordinate in arbitrary log units. In each panel, the top family of the curve shows data with the mask of 335 td, the middle family with the mask of 100 td, and the bottom family with the mask of 25 td in illuminance. The mask was 1.72 deg in diameter and the adapting background was 100 td in illuminance.

from each observer with the highest and the second highest mask illuminance are shifted upwards in arbitrary log units for graphical clarity.

With the incremental mask, the higher the illuminance of the mask is, the larger the magnitude of the overshoot of the masking curve is. This result is consistent with the results obtained with the incremental mask with abrupt onset (Battersby & Wagman, 1959; Boynton, Bush & Enoch, 1954; Boynton & Kandel, 1957; Crawford, 1947). With the increase of the rise time of the mask up to 250 msec, the magnitude of the overshoot becomes smaller, and the temporal delay at which the overshoot reaches its maximum increases, which is also the case in

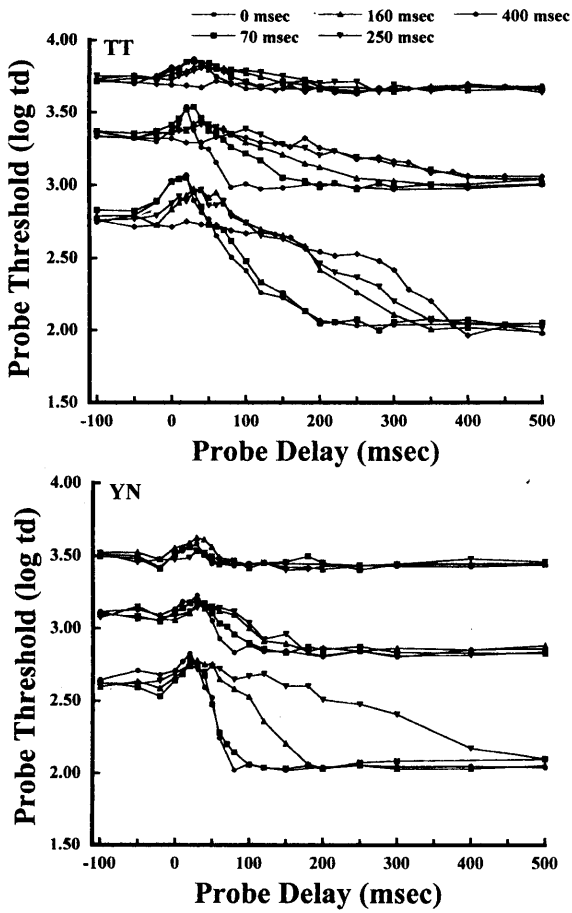

Figure 4. Masking curves for the prolonged decremental mask with variable illuminance. The parameter of the curve is the decay time of the mask. Each panel shows results from different observer. The family of the curve with one mask illuminance is shifted along the ordinate in arbitrary log units. In each panel, the top family of the curve shows data with the mask of -335 td, the middle family with the mask of -100 td, and the bottom family with the mask of -25 td in illuminance. The mask was 1.72 deg in diameter and the adapting background was 435 td in illuminance.

Experiment 1. The threshold overshoot is not present for the mask of the rise time as long as 250 msec, also as the experiment 1.

The threshold overshoot for 0 msec rise time is larger than that for the 70 msec rise time with the highest mask luminance, but these two overshoots are about the same in magnitude with the masks of the two lower luminance values. If the discrimination between the two temporal edges of the luminance increment is determined by the amplitude difference in the initial transient component of the response, this result may be inconsistent with the finding of Bornschein (1962c), who reported that the discrimination between the stimulus with rise time of 7 msec and that with rise time of 100 msec becomes progressively more difficult as the luminance of the stimuli increases from 0.83 to 830 cd/m^2. Bornschein (1962c)'s finding also seems to be inconsistent with the present result that the temporal course of the masking curve tends to slow down as the rise time of the mask is increased, being independent of the mask luminance.

The common sub-peaks of the masking curves with longer rise times to both observers seem to be unclear as the case with Experiment 1.

As is the case with the result of Experiment 1, the magnitude of the overshoot of the masking curve with the decremental mask does not significantly decrease up to the decay time of 70 msec or 160 msec, and essentially disappears with 400 msec of the decay time. The peaks of the curve appears at 20-30 msec, at 30-40 msec, and at 40-50 msec with the decay time of the mask of 0-70 msec, of 160 msec, and of 250 msec, respectively, which is also comparable with the result of Experiment 1. Surprisingly, the magnitude of the threshold overshoots for such decay time of the mask does not change dramatically with the mask luminance. The whole shape of the masking curve slows down with the decay times of 160 msec and more as the case with Experiment 1. Bornschein (1962c) reported that the difficulty of the discrimination between the decremental luminance ramp with the decay time of 7 msec and that of 100 msec decreases with the increase of the luminance from 0.83 to 830 cd/m^2. This is not in accord with the masking data presented here in the point of both the amplitude and the shape of the overshoot.

Discussion

The effect of the size of the step-like luminance change upon the visual response estimated as the masking curve has been well investigated (Baker, Doran & Miller, 1959; Battersby & Wagman, 1959; Boynton & Kandel, 1957; Brooks, Impelman & Lum, 1981; Crawford, 1947; Rinalducci, 1967; Takiura, Takahashi & Maruyama, 1994; von Wiegand, Hood & Graham, 1995). Matsumura (1976, 1977) first obtained the masking curves for the masks with the ramp-like luminance profile as well as with the step-like one. But Matsumura used only one level of the mask luminance, which was considerably higher, for the incremental and the decremental masks, respectively, in each study. In the present experiment, we investigated the effects of the mask luminance with variable rise or decay times, which is lower than that used by Matsumura, upon the masking curve, and showed that the features of the masking curve for the ramped mask are essentially independent of the mask luminance. This result suggests that the temporal response characteristics of the mechanism integrating the stimulus luminous energy or assessing the successive stimulus luminance change is independent of the luminance used in the present experiment and in the studies of Matsumura (1976, 1977) at least under the moderate light adaptation condition.

Decreasing the temporal luminance gradient of the mask causes the great decrease of the magnitude of the overshoot of the masking curve for the incremental mask, but affects relatively small effects upon the magnitude of the transient of the masking curve for the decremental mask. Comparable results were obtained by Takiura, Takahashi and Maruyama (1994) for the step-like luminance mask. In their study it was shown that the threshold overshoot of the probe for the prolonged mask of just above the threshold luminance can be clearly noticed with the decremental mask but is almost completely disappears with the incremental mask. These facts suggest the robustness of the response to the decremental luminance change against the decrease in the luminous energy per unit time. The robustnes of the response to the luminance decrement is also suggested by the results of the neurophysiological studies on the responses of the retinal on-off cells of the amphibians (Gordon & Graham, 1973; Hartline, 1938).

General Discussion

Matsumura (1976, 1977) first investigated the effects of the rate of the stimulus temporal luminance change on the responses of the human visual system using the masking technique. He found that the visual responses psychophysically estimated as the masking curve changes in magnitude and time course with the change of the temporal luminance change: with the decrease of the rate of luminance change, or with the increase of the ramp time, the transient response of the visual system was decreased in magnitude and its whole course became slower. Such change in response was dependent upon the luminance polarity.

In the two experiments reported here, we showed relative independence of the Matsumura (1976, 1977)'s findings from the stimulus spatial extent and luminance, at least under the light-adapted condition. In addition, we also found that the visual response disappears with the longer rise or decay times (250 msec and 400 msec) of the stimulus than those tested by Matsumura (400 msec and shorter). This result suggests that with shorter rise or decay times than 250 msec or 400 msec, the response of the magnocellular pathway is predominant over those of the parvocellular pathway in the visual system, and that with longer ramp times, the parvocellular pathway becomes predominant.

The robustness of the response to the luminance decrement in comparison with the response to the increment was shown by the smaller effect of the decay time on the magnitude of the psychophysically-recorded response than the rise time. This suggests that the supraliminal temporal integration characteristics of the on-channel in the visual system differ from those of the off-channel, and that the response of the off-channel might be more robust than that of the on-channel.

References

Baker, H. D., Doran, M. D., & Miller, K. E. (1959). Early dark adaptation to dim luminances. *Journal of the Optical Society of America*, **49**, 1065-1070.

Bartley, S. H., & Bishop, G. E. (1942). Some features of the optic-nerve discharge in the rabbit and cat. *Journal of Cellular and Comparative Physiology*, **19**, 79-93.

Battersby, W. S., & Wagman, I. H. (1959). Neural limitations of visual excitability. I. The time course of monocular light adaptation. *Journal of the Optical Society of America*, **49**, 752-759.

Battersby, W. S., & Wagman, I. H. (1964). Light adaptation kinetics: the influence of spatial factors. *Science*, **143**, 1029-1031.

Bergen, J. R., & Wilson, H. R. (1985). Prediction of flicker sensitivities from temporal three-pulse data. *Vision Research*, **25**, 577-582.

Bornschein, H. (1961). Der Einfluß der Reizanstiegungszeit auf die Belichtungsantwort der reinen Zapfennetzhaut. *Pflügers Archiv für die gesamte Physiologie des Menschen und der Tiere*, **272**, 528-536.

Bornschein, H. (1962a). Der Einfluß zeitlicher Reizgradienten auf die Impulsaktivität retinaler Neurone der Katze. *Pflügers Archiv für die gesamte Physiologie des Menschen und der Tiere*, **275**, 478-494.

Bornschein, H. (1962b). The response of the human eye to red stimuli with different temporal gradients of luminance. *Acta Ophthalmologica, Supplementum*, **70**, 142-146.

Bornschein, H. (1962c). Die subjektive Unterscheidung zeitlicher Gradienten optischer Reize. *Vision Research*, **2**, 463-467.

Bornschein, H., & Gunkel, R. D. (1956). The effect of rate of rise of photic stimuli on the human electroretinogram. *American Journal of Ophthalmology, third Series*, **42/2**, 239-243.

Bornschein, H., & Schubert, G. (1953). Das photopische Flimmer-Elektroretinogramm des Menschen. *Zeitschrift für Biologie*, **106**, 229-238.

Bowen, R. W. (1989). Two pulses seen as three flashes: a superposition analysis. *Vision Research*, **29**, 409-417.

Bowen, R. W., Mallow, J. V., & Harder, P. J. (1987). Some properties of the double-flash illusion. *Journal of the Optical Society of America, Series A*, **4**, 746-755.

Boynton, R. M. (1966). Vision. In J. B. Sidowski (Ed.) *Experimental methods and instrumentation in psychology* (pp. 273-330.). New York: McGraw-Hill.

Boynton, R. M. (1972). Discrimination of homogeneous double pulses of light. In D. Jameson, & L. M. Hurvich (Eds.) *Handbook of sensory physiology. Volume VII/4. Visual psychophysics* (pp. 202-232). New York: Springer.

Boynton, R. M., Bush, W. R., & Enoch, J. M. (1954). Rapid changes in foveal sensitivity resulting from direct and indirect adapting stimuli. *Journal of the Optical Society of America*, **44**, 56-60.

Boynton, R. M., & Kandel, G. (1957). On responses in the human visual system as a function of adaptation level. *Journal of the Optical Society of America*, **47**, 275-286.

Boynton, R. M., & Miller, N. D. (1963). Visual performance under conditions of transient adaptation. *Illuminating Engineering*, **58**, 541-550.

Boynton, R. M., & Siegfried, J. B. (1962). Psychophysical estimates of on-responses to brief light flashes. *Journal of the Optical Society of America*, **52**, 720-721.

Breitmeyer, B. G. (1984). *Visual masking: an integrative approach*. New York: Oxford University Press.

Breitmeyer, B., & Julesz, B. (1975). The role of on and off transients in determining the psychophysical spatial frequency response. *Vision Research*, **15**, 411-415.

Brooks, B. A., Impelman, M. K., & Lum, J. T. (1981). Backward and forward masking associated with saccadic eye movement. *Perception & Psychophysics*, **30**, 62-70.

Buck, S. L. (1985). Determinants of the spatial properties of cone-rod interaction. *Vision Research*, **25**, 1277-1284.

Budrikis, Z. L., & Lukas, F. X. J. (1979). Phase response of the visual system. *Investigative Ophthalmology and Visual Neuroscience*, **18**, *Supplement* (*ARVO*), 92.

Clynes, M., Kohn, M., & Lifshitz, K. (1964). Dynamics and spatial behavior of light evoked potentials, their modification under hypnosis, and on-line correlation in relation to rhythmic components. *Annals of the New York Academy of Sciences*, **112**, 468-509.

Cogan, A. I. (1992). Anatomy of a flash. 2. The 'width' of a temporal edge. *Perception*, **21**, 167-176.

Crawford, B. H. (1947). Visual adaptation in relation to brief conditioning stimuli. *Proceedings of the Royal Society of London, Series B*, **134**, 283-302.

Curcio, C. A., Sloan, K. R., Kalina, R. E., Hendrickson, A. E. (1990). Human photoreceptor topography. *Journal of Comparative Neurology*, **292**, 497-523.

Drew, G. C. (1937). The variation of sensory thresholds with the rate of application of the stimulus. Ⅲ. The differential threshold for intensity of light. *British Journal of Psychology*, **27**, 297-302.

Enroth-Cugell, C., & Jones, R. W. (1961). Responses of retinal ganglion cells to exponentially increasing light stimuli. *Science*, **134**, 1884-1885.

Enroth-Cugell, C., & Jones, R. W. (1963). Responses of cat retinal ganglion cells to exponentially changing light intensities. *Journal of Neurophysiology*, **26**, 894-907.

Fischer, B., Krause, D., & May, H. U. (1972). Schwellenerregung, zeitliche Summation und Impulsreaktionsfunktion in der Retina der Katze: temporale rezeptive Felder retinaler Ganglienzellen. *Experimental Brain Research*, **15**, 212-224.

Frumkes, T. E., & Sturr, J. F. (1968). Spatial and luminance factors determining visual excitability. *Journal of the Optical Society of America*, **58**, 1657-1662.

Gordon, J., & Graham, N. (1973). Early light and dark adaptation in frog on-off retinal ganglion cells. *Vision Research*, **13**, 647-659.

Hartline, H. K. (1938). The response of single optic nerve fibers of the vertebrate eye to illumination of the retina. *American Journal of Physiology*, **121**, 400-415.

Heggelund, P., Karlsen, H. E., Flugsrud, G, & Nordtug, T. (1989). Response to rates of luminance change of sustained and transient cells in the cat lateral geniculate nucleus and optic tract. *Experimental Brain Research*, **74**, 116-130.

Hood, D. C. (1998). Lower-level visual processing and models of light adaptation. *Annual Review of Psychology*, **49**, 503-535.

Hopp, H. H., & Penzlin, H. (1984). The dependence of trout's electroretinographic response of temporal gradient of luminance. I. The on-response. Zoologische Jahrbücher : *Abteilung für allgemeine Zoologie und Physiologie der Tiere*, **88**, 327-336.

Ishihara, M. (1906). Versuch einer Deutung der photoelektrischen Schwankungen am Froschauge. *Pflügers Archiv für die gesamte Physiologie des Menschen und der Tiere*, **114**, 569-618.

Kitterle, F. L., & Leguire, L. E. (1975). The effect of borders and contours on threshold during early dark adaptation. *Vision Research*, **15**, 1217-1224.

Kitterle, F. L., & Leguire, L. E. (1980). The effect of adapting and test field size upon threshold during early dark adaptation. *Bulletin of the Psychonomic Society*, **16**, 394-396.

Knau, H. (2000). Thresholds for detecting slowly changing Ganzfeldt luminances. *Journal of the Optical Society of America, Series A*, **17**, 1382-1387.

Kühne, W., & Steiner, J. (1880). Ueber das electromotorische Verhalten der Netzhaut. *Untersuchungen aus den Physiologischen Institute der Universität Heidelberg*, **3**, 327-377.

Long, G. E. (1951). The effect of duration of onset and cessation of light flashes on the intensity-time relation in the peripheral retina. *Journal of the Optical Society of America*, **41**, 743-747.

Matsumura, M. (1976). Visual masking by luminance increment and decrement: effects of rise time and decay time. *Tohoku Psychologica Folia*, **35**, 104-114.

Matsumura, M. (1977). Visual responses to luminance increment and decrement of temporal ramp stimuli with different rise and decay time. *Tohoku Psychologica Folia*, **36**, 111-119.

Matsumura, M. (1979). Roles of the stimulus temporal waveform in the visual phenomena. (in Japanese). *Annual Report of the Faculty of Education. Gifu University. Humanities and Social Sciences*, **27**, 103-113.

Merigan, W. H., & Maunsell, J. H. R. (1993). How parallel are the primate visual pathways? *Annual Review of Neuroscience*, **16**, 369-402.

Metzger, W. (1930). Optische Untersuchungen am Ganzfeld. Ⅲ. Mitteilung: Die Schwelle für plötzliche Helligkeitsanderungen. *Psychologische Forschung*, **13**, 30-54.

Mierdel, P., Zenker, H. -J., Marre, E. (1992). Cortical potentials to pattern reversal and luminance onset under ramp stimulation conditions in glaucoma. *Documenta Ophthalmologica*, **80**, 43-50.

Mitov, D. Vassilev, A., & Manahilov. V. (1981). Transient and sustained masking. *Perception & Psychophysics*, **30**, 205-210.

Østerberg, G. (1935). Topography of the layer of rods and cones in the human retina. *Acta Ophthalmologica*, **13**, *Supplementum*, **6**.

Penzlin, H., & Hopp, H. H. (1985). The dependence of trout's electroretinographic response on temporal gradient of luminance. Ⅱ. The off-response. *Biomedica Biochimica Acta*, **44**, 449-454.

Poot, L., Snippe, H. P., & van Hateren, J. H. (1997). Dynamics of adaptation at high luminances: Adaptation is faster after luminance decrements than after luminance increments. *Journal of the Optical Society of America, Series A*, **14**, 2499-2508.

Rashbass, C. (1970). The visibility of transient changes of luminance. *Journal of Physiology*, **210**, 165-186.

Rinalducci, E. J. (1967). Early dark adaptation as a function of wavelength and preadapting level. *Journal of the Optical Society of America*, **57**, 1270-1271.

Ronchi, L. (1958). On the electrical response of the human eye to red stimuli of different time distribution of luminance. *Journal of the Optical Society of America*, **48**, 437-438.

Ronchi, L., & di Francia, T. (1957). On the response of the human eye to light stimuli presenting a spatial or temporal gradient of luminance. *Journal of the Optical Society of America*, **47**, 639-642.

Ronchi, L., & Grazi, S. (1956). The dependence of the human electroretinogram on the shape of the stimulus as a function of time. *Optica Acta*, **3**, 188-195.

Ronchi, L., & Moreland, J. D. (1957). The effect on the human electroretinogram of the distribution of flux in a light stimulus of finite duration. *Optica Acta*, **4**, 31-40.

Sato, T. (1983). Temporal characteristics of pattern detection (abstract in Japanese). *JPA Proceedings of the 47th Annual Convention*, 119.

Sato, T. (1984). Reaction time to sinusoidal patterns (abstract in Japanese). *JPA Proceedings of the 48th Annual Convention*, 140.

Stern, L. W. (1894). Die Wahrnehmung von Helligkeitsänderungen. *Zeitschrift für Psychologie und Physiologie der Sinnesorgane*, **7**, 249-278.

Stromeyer, C. F. Ⅲ., Zeevi, Y. Y., & Kline, S. (1979). Response of visual mechanisms to stimulus onsets and offsets. *Journal of the Optical Society of America*, **69**, 1350-1354.

Takiura, T. (1996). Effects of rise and decay time of flash on brightness difference threshold. *Tohoku Psychologica Folia*, **55**, 19-33.

Takiura, T., Takahashi, M., & Maruyama, K. (1994). A study on nonlinearity of the visual system in response to the flickering stimuli in the low temporal frequency domain. (in Japanese with English abstract). *Japanese Journal of Psychology*, **65**, 190-196.

Tolhurst, D. J. (1975). Reaction times in the detection of gratings by human observers: a probabilistic mechanism. *Vision Research*, **15**, 1143-1149.

Troelstra, A., & Schweitzer, N. M. J. (1963). An analysis of the b-wave in the human ERG. *Vision Research*, **3**, 213-226.

Tulunay-Keesey, U., & Bennis, B. J. (1979). Effects of stimulus onset and image motion on contrast sensitivity. *Vision Research*, **19**, 767-774.

van der Wildt, G. J., & Rijsdijk, J. P. (1979). Flicker sensitivity measured with intermittent stimuli: Ⅱ. Comparison between temporal gradient detection and the "De Lange" curves. *Journal of the Optical Society of America*, **69**, 666-669.

von Wiegand, T. E., Hood, D. C., & Graham, N. (1995). Testing a computational model of light-adaptation dynamics. *Vision Research*, **35**, 3037-3051.

Wang, G.-H. (1937). Latency of cortical and retinal action potentials induced by illumination of the eye. *Archives of Neurology and Psychiatry*, **37**, 772-775.

Wertheimer, M. (1955). The variability of auditory and visual absolute thresholds in time. *Journal of General Psychology*, **52**, 111-147.

Wilson, H. R. (1997). A neural model of foveal light adaptation and afterimage formation. *Visual Neuroscience*, **14**, 403-423.

(Received February 24, 2003)
(Accepted June 26, 2003)